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PHYLOGENY OF THE ARTHROPODA WITH ESPECIAL REFERENCE TO THE TRILOBITES[1]

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THE phylogeny of the Arthropoda has been discussed so often that merely to summarize previous opinions would require an article of considerable length. In a recent number of the NATURALIST,[2] Professor Crampton has reviewed the subject from the standpoint of a student of insects, the most specialized Arthropoda. It may be of interest to see what results are reached when approached from the point of view of a student of the trilobites, the most ancient members of the phylum. The characteristics of trilobites may be summarized as follows:

APPENDAGES

During the last two years I have had occasion to restudy practically all of the known specimens of trilobites whose appendages are preserved. The limbs of twelve species, representing nine genera, are now more or less fully known. Those which leave least to be desired are *Neolenus* from the Middle Cambrian, *Triarthrus, Calymene, Ceraurus,* and *Cryptolithus* from the Middle Ordovician, and *Isotelus* from the Upper Ordovician. Representatives of all three of the orders into which the class is divided are included in this list, which contains examples of both "primitive" and "specialized" trilobites.

The appendages of all these genera, with the exception of *Isotelus,* whose exopodites are still unknown, prove to be constructed on one plan. An articulatory segment

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[1] This is an abstract of a more extensive discussion of the affinities of the trilobites now being published by the Connecticut Academy of Arts and Sciences.

[2] AMERICAN NATURALIST, Vol. 52, 1919, p. 143.

(coxopodite) supports the proximal ends of two branches, an ambulatory endopodite and a setiferous respiratory exopodite. The endopodite consists in all cases of six segments, the terminal one with movable spines on the distal end, usually three in number, but occasionally several. The proximal segment of the endopodite is a basipodite and gives rise to the exopodite, although both branches articulate with the coxopodite. The method of articulation of coxopodite, exopodite, and basipodite is similar to that of the second thoracic limb of the recent *Anaspides,* as figured by Calman. The exopodite is in all cases composed of a flattened shaft, along the posterior margin of which are delicate flattened setæ. The form of articulation of the basipodite, exopodite, and coxopodite indicates that when one of the outer branches moved the other accompanied it, but as the exopodites were always above the endopodites, they appear to have been of comparatively little use in swimming, and were probably chiefly respiratory organs.

All of the trilobites mentioned, so far as their state of preservation will allow determination, have four pairs of limbs of this sort on the cephalon, a pair on each segment of the thorax, and as many pairs on the pygidial shield as there are annulations on its axial lobe. In front of the biramous limbs there is one pair of uniramous, richly segmented, tactile antennules. The ventral membrane of the trilobite was very thin and feebly supported, so that the articulation of the limbs was not with it, but with infoldings of the dorsal shell which extended downward beneath the glabeller and dorsal furrows. The distal end of each of these appendifers fitted into a notch in the upper side of the corresponding coxopodite. A projection of this latter segment extended mesally nearly to the median line, forming endobases which on the cephalon, and usually along the whole of the body, functioned as food-getting organs.

No other parts of the limbs have yet been found, although I have searched diligently through all of the known material preserving the ventral anatomy. Therefore it seems to me that Walcott has not sufficient evidence for the structures he illustrates and describes as epipodites and exites in *Neolenus,* epipodites in *Triarthrus, Calymene,* and *Ceraurus,* and spiral gills in the last two.[3] The presence of none of these things can, in my view, be proved.

There is little modification of the appendages of different parts of the body. The gnathobases of the coxopodites on the cephalon of *Triarthrus* are more jaw-like than those on the remainder of the body, and in the same species the segments of the endopodites of the pygidium and posterior part of the thorax are more triangular than those of the anterior ones. *Cryptolithus* has the thoracic legs bowed backward to form more efficient pushing organs, and in all species with long hypostomata the anterior biramous appendages seem to be more or less degenerate. Thus, *Calymene* appears to have two pairs of very delicate biramous appendages back of the antennules, and the first one or two pairs of gnathobases of *Calymene, Ceraurus* and *Neolenus* seem to be somewhat reduced, but there is no evidence that any pair of appendages is entirely lost. All the evidence seems to indicate that Beecher correctly homologized the cephalic appendages with the antennules, antennæ, mandibles, maxillulæ, and maxillæ of the Crustacea.

FORM OF BODY

Trilobites are always depressed, flattened animals, with a broad head composed of at least five fused segments, a thorax of from two to forty-four free segments, and a pygidium made up of a variable number of undifferentiated segments. The anal opening is at the posterior end of the pygidium, and the growing point just in front of it, as in other arthropods. New segments are introduced into the posterior end of the pygidium during moults, are pushed forward by the introduction of others

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[3] Smithsonian Miscl. Coll., 1918, Vol. 67, No. 4.

behind, and eventually a certain number are freed from the anterior end of the pygidium to form the thorax. Trilobites with an elongate worm-like form have numerous thoracic segments and small pygidia, while many others have few free segments and the pygidium nearly as large as the cephalon. These latter have usually been called more specialized than the former, but it is obvious from the method of introduction of new thoracic segments that the reverse is the case. This opinion is confirmed by a study of the ontogeny, for it is found that in the protaspis the pygidium of any species is proportionally larger than at any later period in life, and that many species pass through a stage in which they are isopygous.

There is a certain amount of evidence that the pygidium was used as a swimming fin, and some species seem to have had sufficiently strong muscles to enable the animal to dart away suddenly when attacked. Trilobites with large pygidia would thus have a certain advantage over the others, and, as a matter of fact, it was this type which persisted longest. The broad depressed body was not as well adapted for a nectic mode of life as a compressed fishlike one would have been, but it is the form which could most easily be kept afloat and propelled with the minimum of effort. The young of all species are circular or broadly oval in outline, and those adults with subequal shields depart least from that form. A fair inference from the above would be that the elongate crawling trilobite was more specialized than the isopygous swimming one.

INTERNAL ANATOMY

Naturally knowledge of the internal anatomy is not as full as could be desired, but what follows appears to be based on reasonably clear evidence.

The mouth is ventral and usually situated back of the middle of the cephalon. Its position depends upon the length of the "upper lip" or hypostoma, and in extreme cases may be at the posterior end of the cephalon. There is evidence from ontogeny and phylogeny of a backward migration of the mouth, coincident with the same movement of the eyes. In both cases this is probably due to the enlargement of the anterior end of the mid-gut. From the mouth the esophagus extends upward and forward to the enlarged mesenteron which occupies the greater part of the large cavity between the hypostoma and glabella. The intestinal canal tapers backward, but no differentiation of the posterior portion has yet been made out. The anus is beneath the posterior end of the axial lobe. The heart is elongate, chambered, branchiopod-like, and in the one species in which it is preserved, extended from the middle of the cephalon to the anterior end of the pygidium. The principal muscles were a dorsal pair of extensors, attached at the posterior margin of the cephalon and anterior ring of the pygidium, and a ventral pair of flexors, both with branches inserted in each segment. All of these organs were within the axial lobe.

COMPARISON WITH OTHER ARTHROPODA

Having thus briefly stated the principal characteristics of the trilobites, the method will be to indicate briefly the similarities which exist between the trilobites and other arthropods, and to show that there is nothing about the bodily form or characteristics of the appendages to negate the possibility of a derivation directly or indirectly of all other classes from that under discussion. It is obvious that in this short paper each class can be treated but briefly.

CRUSTACEA

The trilobites are themselves crustaceans, as is amply proved by their biramous appendages. An attempt will be made to show that they may have been ancestral to the other crustaceans.

In recent years it has been generally considered that the Branchiopoda were more nearly allied to the trilobites than any other living animals. Bernard, the chief proponent of this association, did not consider either subclass derivable from the other. Walcott has more recently stated that the trilobites were derived from the branchiopods and in this has been followed by Crampton. The points of relationship are: in both subclasses the number of segments is not fixed, and in both there are some species which have large numbers of them; both have a well-developed labrum (hypostoma); both have functional gnathobases along the body; the change in metamorphosis of the branchiopod is comparatively small, although *Apus* is by means a "grown up nauplius," as Bernard put it.

So far as these similarities are important, they do show a close relationship of the two groups, but none of them indicates that either is more primitive than the other. When a closer comparison is made, it at once becomes evident that the trilobites are much more primitive than the branchiopods. For example: trilobites have no carapace; some branchiopods do; trilobites have serially similar appendages on all segments, branchiopods have very different appendages on the head from those on the thorax, and some of the abdominal segments lack them entirely; trilobites have antennæ like the other cephalic and trunk appendages, branchiopods have the antennæ highly modified, degenerate, or absent. In other words, branchiopods are in all these respects much more specialized than the trilobites. Finally, the limbs may be considered. Lankester has shown that the schizopodal limb of the higher Crustacea may be explained as derived from one like that of the thorax of *Apus,* and most students of the Crustacea have followed him in considering the phyllopodous limb the most primitive among the Crustacea. This theory has now been completely upset, for Walcott has found several undoubted branchiopods with appendages in the Middle Cambrian, and the best preserved of them (*Burgessia*) show that the limbs were not phyllopodan, but like those of trilobites. The ancient branchiopods having had simple trilobite-like limbs, it can no longer be held that phyllopodan limbs are primitive, and, stripped of their trilobite-like disguise, these wormlike crustaceans may no longer be considered most primitive. The possession of biramous limbs by the branchiopods of the Middle Cambrian, added to their other undoubted likenesses, indicates the possibility that they were derived from the trilobites, although some of them had then already attained the specialized carapace, pedunculate eyes, and limbless hind-body. This possibility is converted into strong probability when one considers the structure of the beautiful *Marrella splendens* Walcott. The head of this "lace-crab" of the Middle Cambrian is obviously highly specialized, but the structure as a whole proves it to occupy an intermediate position between the trilobites and more specialized crustaceans, including the branchiopods. It resembles the higher crustaceans in having the antennæ uniramous, in lacking exopodites on the cephalic appendages, gnathobases on those of the thorax, and in the absence of pleural lobes from the test of the trunk. This animal retains enough characteristics of the trilobites to show that it was derived from them, and has attained enough characteristics of the higher Crustacea to show that it belongs with them. A better connecting link can hardly be expected.

The Copepoda prove, on analysis, to be much more closely allied to the trilobites than had been supposed. All students have remarked upon the many primitive features of the non-parasitic members of this group, but have generally explained them by the sweeping assertion that they must be degenerate. Why, if they are degenrate, do the Copepoda show fewer modifications during development than any other Crustacea except the trilobites? They, instead of *Apus,* represent the "grown up nauplius."

These animals resemble the trilobites in lacking a carapace, in possessing pleural lobes, which, however, are incurved instead of being flattened. The greatest resemblances are, however, in the appendages. All these, except the antennules, maxillæ, and maxillipeds, are biramous, the antennæ and mandibles being especially like those of trilobites. The Copepoda are easily derivable from the latter, even though there are no fossil forms to connect the two groups. Since they lack compound eyes, and show very slight evidence of having ever possessed them, it is even conceivable that they branched off from the Hypoparia, the most primitive of trilobites.

The Ostracoda and Cirripedia are of course highly modified by their somewhat peculiar method of life, but when the young are studied, the characteristics of trilobites are readily observed. In fact, it is really surprising that the trilobite-like character of the crustacean nauplius is so consistently ignored. It has a broad depressed form like a trilobite. It has simple antennules, biramous antennæ, and mandibles like a trilobite, and the gnathobases of the last two function as mouth-organs. An hypostoma is present, and there is a growing point, as is evidenced by the way new segments are added. It is not, it is true, a trilobite, but it looks like a trilobite modified by suppression, and taken in connection with other evidence, certainly does no injury to the theory that the higher Crustacea were derived from the trilobites.

The Malacostraca can be mentioned but briefly. Their most ancient representative whose appendages are known, *Hymenocaris* from the Middle Cambrian of British Columbia, had biramous appendages like those of the trilobites, and most of the modern members of the group have similar ones on some part of the body. As in lower crustaceans, when the exopodites are lost or degenerate, epipodites are developed to replace them, and thus the limbs become variously modified. It is remarkable, however, how close a resemblance there is between the appendages of a trilobite and those of fresh-water syncarids from Tasmania, and even in the Decapoda the seven segments of the walking leg are serially homologous with the seven segments of that of the trilobite. It has frequently been objected to the trilobites as ancestors of the Crustacea, that they had wide pleural extensions and a large pygidium. To the first it may now be replied that some trilobites did get rid of the pleural extensions, but that, on the other hand, most Crustacea retain some remnants of them. I have already shown above that the large pygidium in trilobites was more primitive than the trunk with numerous free segments, and it may further be pointed out that some orders of Isopoda do have a pygidium.

ARACHNIDA

My task in this class is rendered somewhat easier by the fact that the followers of Lankester appear to have accepted his explanation of the descent of the class from the trilobites. While I agree with the general thesis, I must point out that a certain amount of caution must be used, for the connecting links are not nearly so satisfactory as one would like them to be, and the trilobites are not nearly so closely related even to the Merostomata, as they are to the higher Crustacea.

In the first place, while the Trilobita were probably the ancestors of the Arachnida, they do not themselves belong to that class. Lankester advanced six reasons for placing them in the Arachnida, but the first is the only one having any considerable weight, and is the only one which will be discussed here. This point was that they had only one pair, apart from the eyes, of pre-oral appendages, while the Crustacea have two pairs. Researches since Lankester's article was written seem to show that this apparent difference between the Arachnida and Crustacea is not fundamental, for the cheliceræ of the former are probably to be homologized with the antennæ, not the antennules of the latter, so that the mouth is in the same position in relation to the appendages in both groups. Further, the mouth does not occupy a constant position in the trilobites, but with the elongation of the hypostoma, is pushed backward, so that from one to four pairs of appendages may be attached in front of it.

If dorsal tests only be considered, one can pick out an excellent series showing gradations from a trilobite into *Limulus*. Thus, there are in the Middle and Upper Cambrian the Aglaspidæ, with *Limulus*-like head, trilobite-like free thoracic segments, and *Limulus*-like telson. Following the history of the group through the Paleozoic, there is, in the Silurian, *Neolimulus* with a head which is surely that of *Limulus* but which has vestigial facial sutures, and free thoracic segments are present. By Devonian times, the thorax had begun to fuse into a shield, although some of the Pennsylvanian species retained a few free segments at the anterior end of the thorax. This series is so convincing that one must believe that the Xiphosura developed from the trilobites, but a study of the appendages shows that there are greater differences between those of a trilobite and *Limulus* than between those of a trilobite and one of the highest Crustacea.

The greatest difference is in the complete lack, at any stage of development, of the antennules, from which it follows that the anterior shield in the Xiphosura is a cephalothorax in which at least seven segments are incorporated. It is, of course, entirely possible that in one line of evolution of the trilobites the antennules were lost and the antennæ developed as chelicerae, but if the test be applied to the Aglaspidæ, the results are at variance with the expectation. Walcott has found Aglaspidæ with appendages in the Middle Cambrian, and they seem to have five pairs of appendages on the cephalon, two pairs of which are elongate, multi-segmented, tactile antennæ, and biramous appendages are present on the thorax.[4] These animals were still Crustacea, and the development of elongate antennæ instead of chelicerae shows that they were not tending in the direction of the Xiphosura. It is possible, however, that when the appendages of more Aglaspidæ are known, it will be found that some of them showed a tendency to lose the antennules and develop chelicerae.

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[4] Smithsonian Miscl. Coll., Vol. 57, No. 6, 1912.

Some progress has been made toward the connection of the trilobites with the Merostomata, as the Limulava of Walcott are, in a certain sense, intermediate between the two. The Limulava are, however, true crustaceans, for they have five pairs of cephalic appendages, the first of which are elongate uniramous antennules, and also biramous, trilobite-like limbs on the anterior part of the thorax. They are especially trilobite-like in the fact that the antennæ are not elongate tactile organs, but, in *Emeraldella* at least, are biramous. The relationship to the Merostomata is expressed in the shape of the head, body and telson, and the grouping of the cephalic appendages about the mouth. If these animals lost the antennules, developed the antennæ into cheliceræ, added two thoracic segments to the cephalon, modified the appendages, and added a sternal operculum, a merostome would be produced. I think it is obvious that to change a trilobite into a marine arachnid is a more complicated process than to change one into a crustacean of any kind.

To compare the spiders directly with the trilobites may seem somewhat fanciful, yet in some respects the spiders are more trilobite-like than *Limulus* is. On the germ band there is a pair of buds in front of the mouth which probably are antennules. These later fuse to form the rostrum, and the cheliceræ move into a pre-oral position. Moreover, Jaworowski has shown that the pedipalps on the germ band of *Trochosa singoriensis* are biramous. In young spiders the abdomen is segmented, and the anterior segments bear pairs of limb-buds, some of which are later lost, while others develop into lung-books or spinnerets. The number of abdominal segments appears to be variable, from eight to fourteen, another feature which suggests the trilobites. The spiders very probably did not spring directly from this group, but will eventually be traced to it, and not through the Xiphosura.

INSECTA

I quite agree with Crampton that Handlirsch has presented little or no evidence that the Insecta were derived directly from the trilobites. His chief point was that the most ancient known insects, the Palæodictyoptera, were amphibious, and that their larvae, which lived in water, were very like the adult. His second was that the wings of the Palæodictyoptera probably worked up and down only, and that the two main wings were homlogous with rudimentary winglike outgrowths on each segment of the body. These outgrowths resemble the pleural lobes of trilobites, and were considered to have been derived from them. Comstock, who has recently reviewed the question, does not see any evidence that the Palæodictyoptera were amphibious, and I do not think any entomologist or paleontologist has accepted the idea of a direct transformation of pleural extensions of segments of trilobites into wings. The "para-notal" theory certainly does not involve any such conception. That the insects are derived indirectly from the trilobites is, however, entirely possible, and Professor Crampton has marshalled the data for one such possible line of derivation through the Crustacea in the article to which allusion was made in the opening sentences of this essay. Another theory is that advanced by Tothill, who suggested that the Insecta arose through some chilopod-like tracheate, rather than directly from a marine organism. Tothill[5] has pointed out that in the germ band, spiracles appear as early as the limb-buds, and may thus indicate a tracheate ancestor for the insects. This is, of course, discounting the possible effect of acceleration on the embryo, but the whole anatomy of the insects indicates long separation from the marine ancestor. The germ band of the chilopod is somewhat more primitive than that of the insect, for in some species both antennules and antennæ are present, and the maxillæ and first maxillipeds are biramous. The presence of two pairs of antennae does not point directly to the trilobites, but to some offshoot like *Marrella,* and it is possible that the line has been: trilobite, *Marrella*-like marine animal, chilopod-like tracheate, insect.

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[5] *Am. Jour. Sci.*, Vol. 42, 1916, p. 373.

There remain only the Diplopoda, which show a few trilobite-like characteristics, notably their lateral outgrowths and the endopodite-like walking legs on every segment. Antennules are present, antennæ absent, mandibles and maxillulæ much modified, the latter possibly biramous, and maxillæ absent. The most characteristic feature, the possession of two pairs of limbs on each segment on a part of the trunk, can be shown to have arisen comparatively recently (geologically), for Silurian and Devonian fossils which are undoubted diplopods have a test like that of a trilobite and eyes much like those of a *Phacops.* While there are no close connections, there is nothing to show that the Diplopoda could not have been derived from the Trilobita.

SUMMARY

After the above survey, it should appear that the trilobites, particularly in respect to their appendages, are more primitive than any other Arthropoda. The chief modifications in other groups are in the nature of reductions, in the loss of whole appendages, of branches or of segments. Extra segments are sometimes added in certain appendages, and new outgrowths, epipodites, are common among the Crustacea. The trilobites have what seems, at first sight, a peculiar and specialized dorsal test, but now that it has been shown that the pleural lobes may be lost and the pygidium reduced to a single segment, and, chiefly, that the wormlike form is not primitive but secondary, they may be viewed in an entirely new light.

In the oldest fossiliferous rocks, Lower Cambrian, trilobites are plentiful, branchiopods rare, and no other arthropods present. A greater differentiation is seen in the Middle Cambrian fauna, due, however, entirely to the remarkable assemblage found by Walcott at a single locality in British Columbia. In this fauna the Crustacea are represented by trilobites, anostracan and notostracan branchiopods, *Marrella,* Limulava (possible ancestors of the merostomes), Aglaspidæ (possible ancestors of the Xiphosura), and Leptostraca, the most primitive Malacostraca. The Upper Cambrian brought the first true Merostomata. In the Ordovician, Ostracoda and Cirripedia first appear, and in the Silurian the first undoubted Xiphosura, primitive Diplopoda, and Scorpiones. Insecta and air-breathing Arachnoidea, including Araneæ, appear suddenly in the Pennsylvanian (Upper Carboniferous), and the oldest known Chilopoda are found with them. All of the tracheates probably have a long pre-Pennsylvanian history, however, and the record of the fossils is liable to be amplified by new discoveries at any time.

The geological record, so far as it is now available, is in favor of the theory that the other Arthropoda were derived from the trilobites, for although Crustacea were highly diversified by the Middle Cambrian, all other than these were rare, and the trilobites, while they had not reached their highest development, were exceedingly abundant and varied.

If the trilobites were the most primitive arthropods, the question of the ancestry of the phylum resolves itself into a search for the progenitors of the former. What would be the form of the animal from which the trilobite was derived? The depressed form universal in the subclass and the equally universal lateral ("pleural") lobes have already been commented upon. From a study of comparative morphology, it appears that the more ancient trilobites, and the more ancient members of higher families within the subclass, have the most nearly flat form, the narrowest axial, and the widest pleural lobes. Turning to ontogeny, it is found that in most cases the protaspis of any species shows the same characteristics. All these suggest a broad depressed animal with narrow axial portion as the ancestor. Only a few specialized trilobites like the Remopleuridæ and one subfamily of the Cheiruridæ show extensive reduction of the pleural lobes.

A study of the ontogeny of trilobites with both large and small pygidial shields shows that the pygidia are proportionally larger in the protaspis than in the adult, and the more ancient forms pass through a stage in which they are practically isopygous. This suggests that the ancestor had subequal cephalic and abdominal shields. Since the thorax grows by the breaking down of the pygidium, the ancestor should lack free thoracic segments. Curiously enough, among Walcott's remarkable finds in the Middle Cambrian there is an isopygous crustacean without free thoracic segments. It was named *Naraoia* and referred to the Branchiopoda by Walcott,[6] but since it satisfies the theoretical considerations and evidently can not be referred properly to any other subclass, I am inclined to look upon it as the simplest of all trilobites. The specimens so far described are not fully preserved, but the appendages are apparently biramous and trilobite-like, and there are at least three pairs on the head and fourteen on the pygidium. From Agnostidae with subequal shields and two thoracic segments to *Naraoia* with subequal shields and no thoracic segments is but a step. If the pygidium were built up by the coalescence of once free segments, that step would be in the direction of specialization, but since the reverse is the case, the extraordinary conclusion is reached that the simplest trilobite did not look at all like the traditional benthonic round annelid.

The study of the ontogeny of many species of trilobites long ago established the fact that in the ontogeny the eyes, which may be entirely absent in the very young of the simplest oculiferous species, appear first on the anterior margin and during growth move backward on the head. A point which has not been noted is that this movement is correlated with a backward movement of the mouth, as indicated by the increase in length of the hypostoma, and an increase in size of the anterior part of the glabella. There is nothing mysterious about the process, as it is probably due to the increase in the size of the anterior (digestive) portion of the "stomach." This indicates that in the ancestral form the mouth and eyes were close to the anterior margin, and does away with the necessity of the bent annelid to explain their migration. Many of the simpler trilobites are of course blind, as is *Naraoia*.

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[6] Smithsonian Miscl. Coll., Vol. 57, No. 6, 1912, p. 175.

It is true that much of the argument involves the use of principles drawn from the study of ontogeny, but where the ontogeny points to animals which actually exist and helps to explain observed facts, its use seems to be justified. Swinnerton has recently suggested that students of the ontogeny of trilobites have been led into an entirely wrong interpretation because they have not realized that the protaspis, like the nauplius, is a specialized larva adapted to a nektonic mode of life. Since Swinnerton believes that the trilobites are descended from benthonic annelids, one can not but wonder why the nektonic trochophore was not carried over instead of requiring the development of a new and totally different free-swimming larva by the trilobites. All indications derived from the present study are that the primitive trilobites were floating and swimming animals, that their adoption of a crawling habit was a specialization, that the protaspis was nektonic because the adults were, and that the nauplius of recent Crustacea is a similar free-swimming larva because it harks back to ancestral conditions.